

## Germination and Seed Bank Studies of *Macbridea alba* (Lamiaceae), a Federally Threatened Plant

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### ABSTRACT

*Macbridea alba* (Lamiaceae) is a Federally threatened plant endemic to Florida. Seedlings are rarely observed in natural populations, but seed production has been documented. We assessed the germinability of dry-stored seeds and of experimentally buried seeds, and sampled soil to detect a persistent seed bank.

More than 20% of recorded seeds germinated prior to collection, either within the calyx (viviparous seedlings) or after dispersal into the collection bag. This pre-collection germination indicated that a significant percentage of seeds lack innate dormancy. An estimated 87% of dry-stored seeds were germinable for six months following dispersal, but viability of dry-stored and of buried seeds was negligible after one year. No seedlings emerged from soil that was field collected just prior to seed dispersal, indicating no persistent seed bank. Seed viability does not appear to limit establishment, but dry conditions coincident with likely autumn establishment may limit seedling safe site availability.

### INTRODUCTION

Detailed demographic studies provide a sound basis for managing Federally listed plants, but complete information is available for relatively few species (Menges 1986, Schemske et al. 1994). Reliable information about seed and seedling demography is especially difficult to obtain because germination and establishment may occur in discrete, narrow time frames not sampled during pre-determined data collection periods. Further, safe sites for germination and establishment may be transient and rare on the landscape, making detection less likely. However, the likelihood of observing germination and establishment in field conditions may be increased with knowledge about seed ecology, especially environmental requirements for germination, the existence of a dormancy mechanism, and persistence of a seed bank (Guterman 1992).

*Macbridea alba* Chapman (Lamiaceae), white birds-in-a-nest, is a Federally threatened and Florida state endangered plant. It is endemic to the Apalachicola lowlands of the Florida panhandle, and is known from Bay, Gulf, Franklin, and Liberty counties. It occurs in habitats historically maintained by frequent, low-intensity fires (Godfrey and Wooten 1981). Demographic data from 11 populations monitored for 10 years indicate that mortality among adults is low, that flowering decreases with time since fire, and that seedling establishment is rare (unpubl. data, J. Walker and D. White, Kentucky State Nature Preserves Commission). In 1994, flowering plants produced an average of 7.4 (s.e. = 0.9) seeds each in the first reproductive season following spring controlled burns, 20.1 (s.e. = 3.7) two seasons after 1993 controlled burns, and 10.8 (s.e. = 1.5) three seasons following a 1992 controlled burn (Madsen 1999). It appears that the availability of seeds is not the immediate cause for seedling rarity, but low seedling establishment might result from non-viability of seeds or lack of suitable

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safe sites. Alternatively, the apparent lack of seedling establishment may reflect inadequate sampling, either at the wrong times, places, or frequencies.

The purposes of this study were to assess the viability of *M. alba* seeds, predict the likely timing of germination, and ascertain the presence or absence of a persistent seed bank.

## BACKGROUND

*Macbridea alba* Chapman populations occur on both sides of the Apalachicola River [United States Fish and Wildlife Service (USFWS) 1992], but the most vigorous are within the Apalachicola National Forest (USFWS 1992, 1994).

Populations occur in wet to mesic pine flatwoods (USFWS 1994), wet savannas, seepage slopes, and ecotones between pine flatwoods and cypress/ti-ti swamps (Kral 1983, USFWS 1992). The open canopy consists of longleaf pine (*Pinus palustris*) with occasional slash pine (*Pinus elliotii*). Saw palmetto (*Serenoa repens*) and low shrubs, such as *Gaylussacia mosieri*, are often present. Grasses, mainly wiregrass (*Aristida beyrichiana*), less commonly with toothache grass (*Ctenium aromaticum*) and *Panicum* species, dominate the ground layer in regularly burned sites (USFWS 1992). Sedges (e.g. *Scleria pauciflora* and *Rhynchospora plumosa*), and forbs (e.g. *Rhexia alifanus*, *Pityopsis graminifolia*, *Eurybia eryngiifolia*, *Seymeria cassioides*, and *Polygala lutea*) are typical associates. Running oak (*Quercus pumila*), wild indigo (*Baptisia*) (USFWS 1994), and denser longleaf pine are found in drier sites (USFWS 1992). *Macbridea alba* may occur in the vicinity of other rare plant species, including *Verbesina chapmanii*, *Scutellaria floridana*, *Pinguicula ionantha* (USFWS 1994), *Harperocallis flava*, and *Stachydeoma graveolens* (J. Walker and D. White, unpubl. data 1994). Taxonomy follows Kartesz 1999.

*Macbridea alba* is a rhizomatous perennial herb that reproduces vegetatively and by seed. Flowering occurs through a few weeks, beginning anytime from May to August depending on weather and recent fire history. Bisexual flowers with brilliant white corollas are arranged in terminal compressed inflorescences on stems up to 1 m tall. Each flower may produce up to four nutlets, which mature in July, August, or September. Nutlets, referred to as seeds hereafter, are tan, obovoid, and up to 2.5 mm long (Small 1933, Godfrey and Wooten 1981, Kral 1983, USFWS 1994, and Madsen 1999). Seed bank recruits have not been reported.

Although *M. alba* flowers and produces seed in garden conditions without burning (J. Walker and D. Madsen, unpubl. data 1999), prescribed fire is important for maintaining vigor in natural populations. Almost all mature *M. alba* plants survive prescribed fires set in the early spring (February through May). The number of flowers produced per plant peaks either in the growing season following a winter or early spring fire, or in the next season after a later spring (mid-May) fire. Flowering continues but decreases through at least three seasons without burning; in long unburned sites, plants are etiolated and flower rarely if at all. Periodic fire removes aboveground live and dead vegetation and may thereby reduce competition experienced by adults and seedlings (J. Walker and D. White, unpubl. data, 1994; Madsen 1999).

The field sites of this study occur on Dothan, Leefield, Dunbar, and Bladen series loamy sands that are infertile and poorly drained (USFWS 1992, 1994). The mean annual high/low temperature is 26/14°C, with approximately 20 days of freezing temperatures annually (United States Department of Commerce 1984–1993). Average daily high/low temperatures are 33/19°C during seed dispersal in August and 26/12°C in April, the first month in the year with no history of freezing temperatures. Mean annual precipitation is 151 cm, with most of the rain falling January through March and July through August; fall and late spring are the driest seasons.

## METHODS

### *Germination chamber studies*

To investigate the viability and germinability of *Macbridea alba* seeds and the effects of storage, we conducted germination chamber trials at one of two temperature regimes on seeds that were approximately 2, 5, 6, or 12 months old (Table 1). We did not test freshly

**Table 1.** Timeline and summary of methods and results for *Macbridea alba* germination chamber trials. Seeds were collected 27 and 28 August 1994. Ambient and 30/15°C incubation temperatures approximate September field temperatures and 25/10°C approximates April field temperatures. T50 indicates the number of days when 50% of the final percent germination was achieved. Results are means of petri dish replicates  $\pm$  standard errors. See text for details

Incubation Start Date	Seed Age at Start of Incuba- tion (months)	20 Day Pre-trial Stratific- ation	Incubation Day/Night Temper- ature (°C)	# of Petri Dishes	Total # of Seeds	Final % Germin- ation	T50 (days)
25 October 1994	2	no	ambient*	4	30	85.0 $\pm$ 7.5	13.3 $\pm$ 0.9
3 January 1995	5	no	30/15	6	150	70.7 $\pm$ 4.2	23.0 $\pm$ 1.3
8 January 1995	5	no	25/10	6	150	84.0 $\pm$ 3.2	20.5 $\pm$ 0.7
2 February 1995	6	no	30/15	3	75	73.3 $\pm$ 1.6	25.3 $\pm$ 3.6
2 February 1995	6	no	25/10	3	75	68.0 $\pm$ 8.5	22.7 $\pm$ 2.3
2 February 1995	6	yes	30/15	3	75	66.7 $\pm$ 7.1	34.7 $\pm$ 5.9
2 February 1995	6	yes	25/10	3	75	73.3 $\pm$ 9.1	18.3 $\pm$ 2.5
11 September 1995	12	no	30/15	6	150	0.0 $\pm$ 0.0	—

\* We conducted the first 8 days of the pilot germination trial of 2-month-old seeds in a germination chamber set at 30/20°C. Then, due to equipment failure, we transferred dishes to a south-facing windowsill until completion of the trial.

collected seed because germination chambers failed. In the discussion we address the importance of testing fresh seed.

We collected seed for this study from seven populations within the Apalachicola National Forest in Liberty County. Because *M. alba* is federally endangered, our seed collection permit allowed us to keep only 1500 seeds for experimental purposes. To prevent the dispersal of mature seeds and to enable us to calculate seed production (reported in Madsen 1999), we enclosed infructescences in mesh bags on 10, 11, 24, 28, and 29 July 1994, after flowering and prior to seed maturation. On 27 and 28 August 1994 we collected these infructescences, which then contained mature seeds. We tallied seeds that had germinated in collection bags, and discarded them along with seeds that were shriveled or not firm. The final seed pool consisted of firm, filled seeds from 132 plants and seven populations. We stored seeds in an unheated greenhouse that approximated field temperatures, hereafter referred to as dry-storage. Unless otherwise stated, we performed all germination chamber experiments on dry-stored seeds.

We carried out the main germination tests using the following general methods: We sowed replicates of 25 seeds each in covered plastic petri dishes on sand moistened with micropore-filtered water. The petri dishes incubated in germination chambers with temperature regimes that approximated 12-hour day/12-hour night air temperatures at the sites during dispersal in September (30/15°C or 30/20°C) or during April (25/10°C). A daily 14-hour photoperiod began one hour before the day temperature began and ended one hour after the day temperature ended. We tallied germinants and removed germinated seeds, as defined by radicle emergence. To minimize losses to fungal infections, we segregated seeds that developed mildew on their seed coats in separate petri dishes, after immersing them for one minute in a 1% Clorox solution. We checked seeds daily until none germinated for a month.

In January 1995, we stratified a subset of seeds by storing them with moist sphagnum in Ziploc® bags at 2°C. The refrigeration unit was unlighted, but seeds occasionally were exposed to light when the door was opened to remove or introduce other lots of seeds. We began germination chamber tests for stratification effects after 20 days of stratification. One hundred and fifty stratified seeds were not used in this trial and continued to be stored in the freezer for a total of six months. Many of these cold-stored seeds germinated while in storage; those that did not were used as controls for the seed bank study in July 1995.

Because none of the 12-month-old dry-stored seeds from the September 1995 trial germinated, we tested this lot ( $n = 132$  non-decayed seeds after the germination trial) with tetrazolium (Moore 1973) on 16 November 1995 to determine if they were viable but dormant. In

order to interpret the tetrazolium test results correctly, on 21 September 1996 we tested freshly matured seeds ( $n = 30$ ) produced from the first seed crop of the Clemson research population of *M. alba* plants.

We calculated final percent germination and we used the number of days when 50% of final percent germination was achieved (T50) to represent germination rate (*sensu* Thanos et al. 1989). We calculated means and standard errors treating petri dishes as replicates. We performed analyses of variances (ANOVAs) (SAS 1989–1996) to test for significant treatment effects on final germination percentage and T50. Analyses included one-way ANOVAs for the effect of age (two, five, and six months; not stratified) at 30/15°C or equivalent temperatures; two-way ANOVAs to determine the main effects and interactions between incubation temperature (30/15 and 25/10°C) and stratification (stratified and not stratified) of six month old seeds; and two-way ANOVAs to evaluate main effects and interactions between seed age (five and six months; not stratified) and incubation temperature (30/15 and 25/10°C). We log transformed values for T50 to achieve a normal data distribution and report  $p$  values from Type III sum of squares because data set sizes were not equal (SAS 1989–1996).

#### Seed bank studies

To determine the presence or absence of a persistent seed bank, we examined seedling emergence from soil cores collected from within populations in Apalachicola National Forest on 6 and 7 July 1995, just prior to seed dispersal. We collected 300 soil cores, 150 from each of two populations that both had good seed production the previous year (Madsen 1999) and had not been burned since the last cohort of seeds had been dispersed. We extracted ten 15.7 cm<sup>3</sup> cylindrical cores (5 cm deep  $\times$  2 cm diameter) from within 1 m of individual reproductive *M. alba* plants, sampling the vicinity of 15 plants at each site and avoiding plants from which we had collected seeds the previous year. We collected 27 control cores (assumed to be free of *M. alba* seeds) approximately 100 m from a known *M. alba* site. We kept all cores in a cold-room until transferring them to a greenhouse bench on 14 July 1995.

We spread out individual cores over sand in pots with core layers thin enough to ensure that any seeds would be exposed to light. Using control cores, we established nine replicates each for three types of controls: (1) 10 one-year-old dry-stored seeds added to each core, (2) 10 one-year-old stratified (for six months) seeds added per core, and (3) no seeds added. We added seeds to controls to model the emergence phenology and success of *M. alba* seedlings under the greenhouse test conditions. We used one-year-old seeds from dry-storage as well as stratified-storage because dry-stored seeds, which experienced approximate field temperatures, might show germination responses more similar to a natural seed bank than stratified-stored seeds, but stratified-stored seeds may be more germinable (Baskin and Baskin 1998). We monitored controls with no added seeds to verify that no germinable *M. alba* seeds were present in field collected control cores. Mist irrigation kept soil moist throughout the trial. We tallied and marked emerged seedlings twice a week until no seedlings emerged for several weeks.

#### Garden burial studies

To estimate the time of year in which buried seeds are lost from the seed bank to germination or decay, we created an artificial seed bank. On 28 August 1997 we placed into each of 12 fine mesh bags 50 freshly matured seeds from the research population maintained at Clemson University, which were grown from a subset of 1994 field collected seeds. Each bag contained seeds from at least 10 mothers. In previous studies (Madsen 1999), *M. alba* seedlings emerged from seeds buried 2.5 cm deep but not 5 cm. We buried seeds 5 cm deep to maximize the possibility that burial at this depth might induce or enforce dormancy. It is plausible for seeds to be buried this deep in field conditions under tree tip-up mounds or by crayfish. We buried each bag in a 7.5 cm layer of native soil over a soil-less mix (one part peat moss : one part perlite plus gypsum at 6 kg/m<sup>3</sup>) in pots (26 cm diameter  $\times$  27.5 cm deep). The pots were maintained out-of-doors at the South Carolina Botanical Garden. We exhumed three replicates near the calendar start of each season: winter, 16 December 1997

(seed age = 3.5 months); spring, 16 March 1998 (age = 6.5 months); summer, 29 June 1998 (age = 10 months); and fall, 22 September 1998 (age = 13 months). Upon exhumation, we examined each replicate for germinants, rotted seeds, and whole firm seeds, which we tested for viability with tetrazolium.

## RESULTS

### *Germination chamber studies*

In all populations from which we collected seeds, a significant percentage of seeds germinated while the collection bags remained on infructescences in the field. Out of all collected seeds ( $n = 1788$ ), 20.4% had germinated prior to collection. We occasionally observed germinated seeds within calyces of unbaggd infructescences.

Seed viability was high in seeds up to six months old (Table 1, Figure 1). Among the main germination trials, 5-month old seeds incubated at 25/10°C showed 84.0% germination, the greatest final percent germination among the main germination trials. Based on percent germination prior to collection and the greatest observed main trial germination rate, 1994 field-collected seed were a maximum of 87% germinable.

Dry-stored seeds declined in germinability with time and were not germinable a year after collection. Among trials of 2, 5, and 6-month-old seeds incubated at 30/15°C or equivalent ambient temperature, ANOVAs indicated that age significantly affected germination rate ( $F_{(2,10)} = 24.47$ ,  $p < 0.001$ ), but not final percent germination ( $F_{(2,10)} = 2.72$ ,  $p = 0.114$ ). A Tukey multiple comparison test verified that the germination rate of 5- and 6-month old seeds was significantly slower than 2-month old seeds. Final average percent germination was greater in 2-month old seeds than 5- and 6-month old seeds, but the difference was not significant because of high variability among small replicates of 2-month old seeds. Of 12-month old seeds ( $n = 132$  remaining intact seeds), 4.2% ( $\pm 1.7$  s.e.) stained weakly (pink) to tetrazolium, indicating possible viability. In contrast, 100% of freshly matured seeds ( $n = 30$ ) from the Clemson research population stained strongly positive (red), indicating that all seeds were likely viable.

There was no significant main effect of 20 days of stratification on final percent germination or on germination rate (T50) of 6-month old seed, while incubation temperature and its interaction with stratification did affect germination rate (Table 2). The results of a least squares means multiple comparison test indicated that the germination rate for stratified seeds incubated at 30/15°C was significantly slower than for stratified seeds incubated at 25/10°C as well as non-stratified seeds incubated at 25/10°C. After six months of stratification, 40% ( $\pm 9.0$  s.e.) ( $n = 6$  stratification bags; total seeds = 150) had germinated at 2°C.

There was no significant main effect of temperature on germination of five and six month old dry-stored seed (Table 3). However, there was an interactive effect of temperature and seed age on germination. According to least squares means multiple comparison tests, lower temperatures significantly enhanced final percent germination of seeds stored five months, but not in seeds stored six months.

### *Seed bank studies*

No seedlings of *Macbridea alba* emerged from soil cores collected adjacent to *M. alba* plants just prior to seed dispersal. Control cores, collected outside a *M. alba* population, varied in seedling emergence, depending on the type of control treatment. No *M. alba* seedlings emerged from controls with no added seeds or from controls with added dry-stored seeds. *Macbridea alba* seedlings did emerge from eight of nine cores with added 6-months-stratified seeds; of the 90 stratified seeds sown, 31.1% ( $\pm 5.1$  s.e.) emerged.

### *Garden burial studies*

At the beginning of winter, 22% ( $\pm 2.2$  s.e.) of seeds buried three and a half months previously were still whole and firm (Table 4). About half of these stained red to tetrazolium, indicating they likely were viable; others stained pink and it is unknown if they were viable.

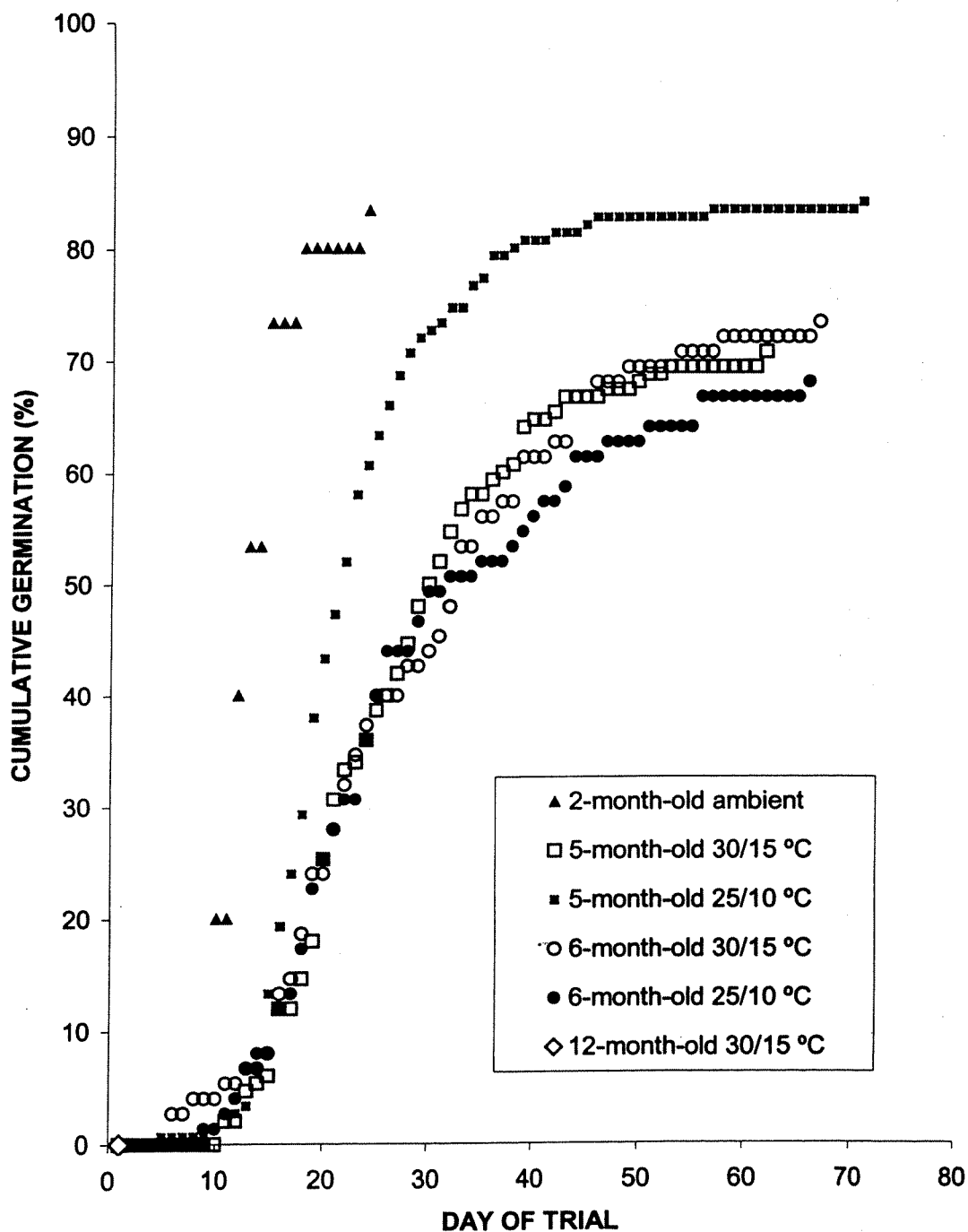


Figure 1. Cumulative percent germination for *Macbridea alba* seeds of differing ages and incubation temperatures. Seeds were collected late August 1994 and stored dry until each trial. N = 30 seeds for two-month-old seeds; n = 150 seeds for each treatment of five-month old seeds, n = 75 seeds for each treatment of six-month-old seeds; n = 150 seeds for 12-month-old seeds. See text for details.

**Table 2.** ANOVA summary for the effects of incubation temperature, stratification, and their interaction on final % germination and germination rate, T50, in *Macbridea alba*. The table compares germination for four treatments: stratified vs. non-stratified seeds incubated at 30/15°C vs. 25/10°C. Data are from the trials of 6-month-old seeds. N = 3 dishes for each treatment. Dishes contained 25 seeds each. See text for details

Dependent Variable	Source of Variation	df	Type III Sum of Squares	Mean Square	F Value	p
Final % Germination	temperature	1	1.33	1.33	0.01	0.913
	stratification	1	1.33	1.33	0.01	0.913
	temp. × strat.	1	108.00	108.00	1.04	0.338
	error	8	832.00	104.00		
	total	11	942.67			
T50	temperature	1	0.41	0.41	10.71	<b>0.011</b>
	stratification	1	0.01	0.01	0.16	0.696
	temp. × strat.	1	0.21	0.21	5.47	<b>0.048</b>
	error	8	0.30	0.04		
	total	11	0.92			

Results suggest a viable experimental seed bank at the beginning of winter of at least 12%, and possibly as high as 20% (including red and pink staining seeds) of the initial seed cohort. Confirmed viability, indicated by the number of germinated seeds plus red-staining seeds, was 46% in early winter and less in subsequent exhumations. Percentages of missing seeds represent germinated or ungerminated seeds that decayed completely or beyond recognition prior to exhumation.

## DISCUSSION

The number of *Macbridea alba* seedlings observed in natural populations is not limited by seed viability, at least of fresh seed as a factor by itself. Of course, seed viability may vary from year to year (King 1989, Houle and Payette 1991, Pierce and Moll 1994) or from population to population (King 1989, Halward and Shaw 1996). Also, the high germination rates found in the laboratory undoubtedly overestimate seedling emergence in the field (Nault and Gagnon 1993), where mortality due to factors such as inconsistent moisture or pathogens often prevent emergence (Guariguata and Azocar 1988). Monitoring seeds sown in natural

**Table 3.** ANOVA summary for the effects of seed age, incubation temperature, and their interaction on final % germination and germination rate, T50, in *Macbridea alba*. The table compares germination for four treatments: 5-month-old vs. 6-month-old non-stratified seeds incubated at 30/15°C vs. 25/10°C. N = 6 dishes for each treatment of 5-month-old seeds and n = 3 dishes for each treatment of 6-month-old seeds. Dishes contained 25 seeds each. See text for details

Dependent Variable	Source of Variation	df	Type III Sum of Squares	Mean Square	F Value	p
Final % Germination	temperature	1	64.00	64.00	0.90	0.358
	age	1	177.78	177.78	2.51	0.136
	temp. × age	1	348.44	348.44	4.92	<b>0.044</b>
	error	14	992.00	70.86		
	total	17	1582.22			
T50	temperature	1	0.05	0.05	2.84	0.114
	age	1	0.03	0.03	2.10	0.169
	temp. × age	1	0.00	0.00	0.00	0.963
	error	14	0.23	0.02		
	total	17	0.31			

Table 4. Germination and viability of *Macbridea alba* seeds experimentally buried in pots at the South Carolina Botanical Garden. Twelve bags containing 50 freshly matured seeds each were buried 28 August 1997. Three bags were exhumed at the end of each season. Observed germinants = seedlings or seeds with emerged radicles. Whole firm seeds were tested with tetrazolium (red staining indicates likely viability; pink staining indicates possible viability). Decayed seeds = recovered seeds that were not whole or firm. Missing seeds are those not visually accounted for in other categories. All percentages are means ( $\pm$  s.e.) for  $n = 3$  bags per exhumation date. See text for details

Date Exhumed	Seed Age (months)	% Observed Germinants	Whole, Firm Seeds				
			% Red Staining	% Pink Staining	% Not Staining	% Decayed	% Missing
16 December 1997	3.5	34.0 $\pm$ 4.2	12.0 $\pm$ 2.0	8.0 $\pm$ 3.1	2.0 $\pm$ 2.0	12.7 $\pm$ 2.4	31.3 $\pm$ 4.6
16 March 1998	6.5	16.6 $\pm$ 6.4	0.0 $\pm$ 0.0	4.7 $\pm$ 1.8	8.0 $\pm$ 1.1	4.7 $\pm$ 3.7	66.0 $\pm$ 9.0
28 June 1998	10	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	2.0 $\pm$ 1.2	3.3 $\pm$ 2.4	0.7 $\pm$ 0.7	94.0 $\pm$ 3.1
22 September 1998	13	0.7 $\pm$ 0.7	0.0 $\pm$ 0.0	1.3 $\pm$ 1.3	2.0 $\pm$ 2.0	7.3 $\pm$ 2.9	88.7 $\pm$ 4.1

populations for multiple years will be required to detect seedling emergence rates and estimate germination rates in field conditions.

The observed loss of viability in cohorts of experimentally buried seeds over a 13-month period is consistent with the absence of a persistent seed bank in *M. alba*. In addition to seed mortality, the seed bank likely was depleted in part by germination, including fatal germination from germinating too deeply (Houle and Payette 1991, Murdoch and Ellis 1992). *Macbridea alba* seeds readily germinate while buried at a depth of 5 cm, but this is a depth from which this species' cotyledons are unable to emerge (Madsen 1999). That a small percentage of 13-month old experimentally buried seeds and dry-stored seeds were possibly viable, as indicated a chemical test, is not strong evidence that a persistent seed bank may be possible.

Our results provide some information about possible dormancy mechanisms in *M. alba* seeds. First, most *M. alba* seeds appear to lack an innate dormancy mechanism, as evidenced by the percentage of collected seeds that germinated within the calyx or in collection bags. Of all seeds produced, including seeds germinated in collection bags, only about 13% of seeds that were six-months old or younger did not germinate. The failure of all 1-year-old dry-stored seeds to germinate likely reflected a loss of viability, rather than evidence of a dormant state, because the small percentage that stained positive to tetrazolium did so weakly. Though results strongly suggest a lack of innate dormancy, it is possible that a portion of the seed cohort was dormant at dispersal and that the seeds became non-dormant or conditionally dormant in the two months prior to the first germination test. Seeds of some species can be essentially dormant (i.e. a small portion may germinate, but often slowly), but after-ripen in as short as two months (Baskin and Baskin 1982) and during dry-storage (Probert 1992). To eliminate this uncertainty, fresh seeds must be tested. Second, the finding that 12.0  $\pm$  2.0% of seeds experimentally buried at the end of summer stained strongly to tetrazolium three and a half months later, indicates that some seeds may have a short term dormancy mechanism, or alternatively that burial prevents germination for some otherwise germinable seeds. These *ex situ* tests are imprecise at describing dormancy dynamics in natural populations because environmental factors such as moisture, light, oxygen and nitrate concentrations, and temperature can interact to alter the expression of dormancy and germination responses; seeds may fluctuate in and out of dormancy; and the existence and degree of dormancy may vary within a species (Baskin and Baskin 1998).

Seed dormancy tends to be associated with species living in unpredictable or patchy environments, in species with infrequent opportunities for reproduction (Fenner 1985, Rees 1994), and where seedlings are not likely to survive environmental conditions following dispersal (Baskin and Baskin 1985, Fenner 1985). Lack of seed dormancy is not unusual, particularly for long-lived species in stable environments (Rees 1994). *Macbridea alba* is a



perennial with known individuals surviving for at least seven years. Its habitat is stable in that the disturbance regime of frequent low intensity fires, historically lightning fires and now prescribed fires conducted at least every four years, maintains the habitat structure within acceptable bounds for *M. alba*'s persistence from year to year, and does not kill individuals (J. Walker and D. White, unpubl. data 1994). Maintaining a persistent seed bank of dormant seeds would not seem to be advantageous for *M. alba*; results of seed bank and seed burial investigations are consistent with this prediction.

The results of our germination studies suggest that the most likely time to observe new seedlings in the field would be in the fall. We found that seeds can germinate upon dispersal, which varies from July to September, and most experimentally buried seeds germinate before the onset of winter. Emergence occurs in 10 to 23 days and true leaves develop within the following 40 days (Madsen, pers. obs. 1994). However, fall is a relatively dry season at natural population sites (USDC, 1984–1993) and seedlings are at risk of desiccation during this time. The best conditions for seedling establishment may occur during the occasional wet fall. Our results suggest alternative strategies may be possible: seed burial studies show that some *M. alba* seeds may be dormant through the fall, and incubation temperature and stratification studies indicate that seeds are able to germinate in the cool temperatures of winter or early spring, when rain is more regular.

Our findings suggest some management guidelines for conserving *M. alba*. The lack of dormancy and absence of a persistent seed bank argue for preserving established plants. If management practices eliminate established individuals after the transient seed bank has been depleted, the population cannot re-establish itself; seeds or plants will have to be provided. Additionally, *M. alba* seeds will not remain viable under simple dry-storage conditions at field temperatures, although the cool moist conditions of stratification did prolong viability to some extent for up to six months. For this reason, preserving genetic diversity in an *ex situ* facility may be difficult. As is so often the case, conserving this species *in situ* may be the best option.

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